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ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

Feeding ecology of the walleye (Percidae, *Sander vitreus*), a resurgent piscivore in Lake Huron (Laurentian Great Lakes) after shifts in the prey community

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Abstract

Recovering populations of piscivores can challenge understanding of ecosystem function due to impacts on prey and to potentially altered food webs supporting their production. Stocks of walleye (Percidae, *Sander vitreus*), an apex predator in the Laurentian Great Lakes, crashed in the mid-1900s. Management efforts led to recovery by 2009, but recovery coincided with environmental and fish community changes that also had implications for the feeding ecology of walleye. To evaluate potential changes in feeding ecology for this apex predator, we assessed diets in the main basin of Lake Huron and in Saginaw Bay, a large embayment of Lake Huron, during 2009–2011. Walleye switched their diets differently in the main basin and Saginaw Bay, with non-native round goby (Gobiidae, *Neogobius melanostomus*) and rainbow smelt (Osmeridae, *Osmerus mordax*) more prevalent in diets in the main basin, and invertebrates, yellow perch (Percidae, *Perca flavescens*) and gizzard shad (Clupeidae, *Dorosoma cepedianum*) more prevalent in diets in the bay. Feeding strategy plots indicated that there was a high degree of individual specialisation by walleye in the bay and the main basin. Bioenergetic simulations indicated that walleye in Saginaw Bay need to consume 10%–18% more food than a walleye that spends part or all of the year in the main basin, respectively, in order to achieve the same growth rate. The differences in diets between the bay and main basin highlight the flexibility of this apex predator in the face of environmental changes, but changes in diet can alter energy pathways supporting piscivore production.

KEYWORDS
alewife, diet overlap, feeding strategy, Saginaw Bay, *Sander vitreus*

1 | INTRODUCTION

Resurgent populations of apex piscivores in an ecosystem represent a management success, but at the same time bring about new challenges because of their strong ecosystem impacts. In particular, resurgent predator populations can have strong impacts on their prey community (Baum & Worm, 2009; Hartman, 2003; Link, 2002; Walter & Austin, 2003), which often differs from that which existed prior to the predator's decline. Although changes in the prey community can represent an impediment to piscivore recovery (Nobriga & Feyrer, 2008; Saunders, Hachey, & Fay, 2006), successfully rehabilitated piscivores may also successfully rely on different pathways than before their collapse (Walter & Austin, 2003).

Walleye (Percidae, *Sander vitreus*) are an important commercial and recreational species as well as an important ecological species as an apex predator throughout their native and introduced range in North America. Understanding walleye feeding ecology in the face of environmental changes is important because this apex predator is such

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an ecologically important species in many large North American water bodies. In the Laurentian Great Lakes, including Lake Huron, walleye are native and are found in nearshore areas and in embayments (Fielder, Liskauskas, Gonder, Mohr, & Thomas, 2010). Lake Huron once supported a large commercial fishery targeting walleye, second only to that of Lake Erie in the entire Great Lakes (Schneider & Leach, 1979), but stocks crashed in the mid-1900s due to various factors, including overfishing, loss of habitat and decline in water quality (Fielder et al., 2010; Schneider & Leach, 1979). Historically, the majority of the walleye harvest in Lake Huron came from Saginaw Bay (Baldwin & Saalfeld, 1962), a large, eutrophic embayment that accounts for 5% of the area of Lake Huron. In Saginaw Bay, a recovery programme centred on stocking efforts began in the 1980s, but in 2003, natural reproduction of walleye increased dramatically. In turn, stocking ceased in 2006 and pre-identified recovery metrics were met in 2009 (Fielder et al., 2010; Johnson, He, & Fielder, 2015).

Walleye recovery in Saginaw Bay has been linked to the collapse of non-native alewife (Clupeidae, *Alosa psuedoharengus*) in Lake Huron in 2003 (Fielder, Schaeffer, & Thomas, 2007). Previously, large numbers of alewife migrated into Saginaw Bay for spawning and young alewife used the bay as nursery habitat. Due to their overlap and high abundance, alewife served as an important prey for walleye in Saginaw Bay (Haas & Schaeffer, 1992), but they were also potentially an important predator on larval walleye (Brooking, Rudstam, Olson, & VanDeValk, 1998). The collapse of alewife in the main basin has been linked to high predator pressure as well as bottom-up factors such as the nearly complete disappearance of the high-energy benthic amphipod *Diporeia* spp. (He et al., 2015). Coincident with the alewife collapse, a variety of other ecosystem changes occurred in Lake Huron and Saginaw Bay during the early 2000s, with potential important implications for walleye feeding ecology. (i) Native yellow perch (Percidae, *Perca flavescens*) recruitment also increased dramatically in Saginaw Bay, but survival to age-1 has been poor, possibly in part due to walleye predation (Ivan, Thomas, Höök, & Fielder, 2011). (ii) The invasive round goby (Gobiidae, *Neogobius melanostomus*) increased in abundance in the main basin of Lake Huron and Saginaw Bay during 1997–2003 (Schaeffer, Bowen, Thomas, French, & Curtis, 2005). (iii) Finally, Lake Huron became increasingly oligotrophic (Cha, Stow, Nalepa, & Reckhow, 2011), and while Saginaw Bay remained eutrophic, nutrient and chlorophyll concentrations in the bay have decreased and the bay's fish community has shifted towards species less tolerant of eutrophic conditions (Ivan, Fielder, Thomas, & Höök, 2014). These unintended ecosystem changes provide a useful opportunity to evaluate the ecological plasticity of fishes, including an important apex predator like walleye.

As walleye recovered in Saginaw Bay, the walleye population expanded its range into the main basin of Lake Huron (He et al., 2015). Presently, about 40% of the Saginaw Bay spawning stock migrates into the main basin after spawning season with most returning in late fall (Hayden et al., 2014). While residing in either Saginaw Bay or Lake Huron, walleye are presumably exposed to differing prey assemblages (Fielder & Thomas, 2014; Roseman, Chriscinske, Castle, & Bowser, 2015) and thermal environments (Peat et al., 2015). Prey types can vary in energy content, which in turn can influence the condition, growth and consumption requirements of their predators (Madenjian et al., 2000; Pothoven & Madenjian, 2008; Pothoven et al., 2006). He et al. (2015) coupled a stock assessment model with a bioenergetics model to estimate that annual consumption of prey fish by walleye residing in Lake Huron's main basin increased about threefold during 2003–2008. However, important details on walleye diet in the main basin of Lake Huron during 2003–2011 were not specifically addressed by He et al. (2015), and walleye diet in Saginaw Bay was not addressed at all in their study.

The primary goal of our study was to characterise the feeding ecology of walleye sampled from Saginaw Bay or the main basin of Lake Huron after the 2003 collapse of the alewife population in Lake Huron. Walleye diets can shift rapidly in response to changes in the prey community (Haas & Schaeffer, 1992; Hartman & Margraf, 1992; Knight & Vondracek, 1993), but diet shifts could represent changes in energy pathways and could vary among ecosystems. The specific objectives of our study included the following: determine the diet composition of age-2 and older walleye from both Saginaw Bay and the main basin of Lake Huron, determine whether diet composition of the walleye varied significantly between these two regions, assess the degree of diet overlap between these two regions, characterise the feeding strategy (specialist vs. generalist feeding) of walleye from both regions, and use bioenergetics modelling to determine the effects of differences in water temperature regimes and diet composition between the two regions on walleye feeding rate. In addition, we compared our findings with the available data on walleye diet in Saginaw Bay and the main basin of Lake Huron prior to the alewife collapse of 2003 to evaluate how diets have changed over time.

2 | METHODS

Sampling took place during April to November in 2009–2011 throughout Saginaw Bay and in 2010–2011 along the north-west and south-east regions of the main basin of Lake Huron (Fig. 1). Walleye were collected using various gill nets set overnight and with daytime bottom trawls as part of assessments carried out by the Michigan Department of Natural Resources, Ontario Ministry of Natural Resources, Chippewa Ottawa Resource Authority, National Oceanic and Atmospheric Administration, and the United States Fish and Wildlife Service.

Upon capture, fish were measured to the nearest mm (TL) and weighed to the nearest g and stomachs were removed and frozen. In the laboratory, stomach contents were examined under magnification and prey were identified. Fish were identified to species where possible using bony structures to aid in identification (Traynor, Moerke, & Greil, 2010). Invertebrates were identified to the lowest practical level and were combined into a single category for most analyses. Each prey type from a stomach was weighed to the nearest 0.01 g. Total or standard lengths of fish found in stomachs were measured. Standard lengths were converted to total length using regressions derived from fish caught in Saginaw Bay or from the literature (Carlander & Smith, 1945; Elliott et al., 1996).

FIGURE 1 Map of Lake Huron showing approximate location of sampling locations within the main basin and Saginaw Bay

Diet analysis was restricted to fish age-2+, based on fish length at age for each month estimated from a subset of fish aged using scales. Diets were further separated into two time periods, an early period of April–mid-June, and a late period of mid-June–November. This separation was chosen based on the approximate timing of the migration in mid-June of some walleye out of Saginaw Bay (Peat et al., 2015). Diet was summarised as the percent of total measured prey weight and as frequency of occurrence for walleye in each region and time period. Total length of fish prey that were common to each region was compared using ANCOVA. For this analysis, total lengths of a particular prey found in individual walleye stomachs were the response variable and individual walleye total lengths were the covariate. To provide an indication of fullness, the g food/g fish was determined for individual walleye that had food in their stomachs. This fullness indicator was compared between regions for each time period using ANOVA.

Analysis of similarities (ANOSIM) was used to test for differences in diet assemblages between Saginaw Bay and the main basin of Lake Huron for each time period. Diet assemblages were also compared for walleye collected in the northern and southern halves of the main basin. The ANOSIM approach is analogous to an ANOVA, with a nonparametric permutation applied to a rank similarity matrix of samples (Clarke & Warwick, 2001). Diet composition, standardised as per cent of total wet food weight for each fish, was square root transformed and used to create a Bray–Curtis similarity matrix for ANOSIM. *R*-values from ANOSIM were used as a measure of absolute separation of diet assemblages between regions and are generally more informative than the *p*-values derived from the analysis (Clarke & Gorley, 2001). *R*-values range from −1 to +1, and generally lie between 0 where groups are indistinguishable and +1 where there is high separation among groups. *R*-values <.25 indicate little separation between groups, *R*-values of .5–.75 indicate some overlap between groups and *R*-values >.75 indicate clear separation between groups (Clarke & Gorley, 2001). A similarity percentage routine (SIMPER) was applied to determine which prey discriminated the diet of walleye between regions for each time period. ANOSIM and SIMPER were performed using Primer v5.2.9.

To evaluate the feeding strategy of walleye, an approach proposed by Amundsen, Gabler, and Staldvik (1996) was used, where the prey-specific abundance (P_i) was plotted against the frequency of occurrence. Prey-specific abundance is the percentage a prey type comprises of all prey items in only those predators in which the prey occurs (Amundsen et al., 1996). We used prey-specific diet biomass to determine the percentage contribution by prey. The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and rare prey in the lower left. The vertical axis represents the feeding strategy of the predator in terms of specialisation and generalisation. Predators specialise on prey types in the upper half of the plot, whereas prey types in the lower

half of the plot represent a generalised feeding strategy. Prey points in the upper left indicate specialisation by individuals, whereas points in the upper right indicate a dominant prey of the overall population (Amundsen et al., 1996).

To estimate the implications of potentially differing diets in Saginaw Bay and the main basin of Lake Huron, we used the Wisconsin Fish Bioenergetics 3.1 model (Hanson, Johnson, Schindler, & Kitchell, 1997) to estimate consumption by an age-5 walleye, which corresponded to the average length of walleye used for diet analysis. Consumption was determined for April to November for three scenarios: walleye spent the entire period in Saginaw Bay, walleye spent the entire period in Lake Huron, and walleye spent the early period in Saginaw Bay and the late period in the main basin of Lake Huron to simulate fish that migrate out of the bay after spawning (migration on 16 June). We assumed a starting weight of 816 g and an ending weight of 963 g for model simulations based on weight estimates from 2009 to 2011 from a time-varying growth model used in He et al. (2015) after accounting for growth between early September and April (D. Fielder, Michigan Department of Natural Resources, personal communication). Limited data exist for walleye growth outside of Saginaw Bay, so growth was assumed to be the same between regions (He et al., 2015). Walleye energy density was based on determinations for fish from Saginaw Bay in 2009–2011 (He et al., 2015) and was assumed identical between regions as no other data were available. Diet composition for each region and time period from this study was used for diet inputs. Prey energy density was based on direct energy density determinations from fish caught in Saginaw Bay (2009–2010) or Lake Huron (2007–2009) (see Appendix) or from published results (Table 1). Monthly mean water temperature for the main basin was determined from 2012 to 2013 data from the National Data Buoy Center buoy 45162 located in northern Lake Huron in 20 m of water in Thunder Bay and from National Data Buoy Center buoy 45163 in 14 m of water in Saginaw Bay (www.ndbc.noaa.gov) (Fig. 2).

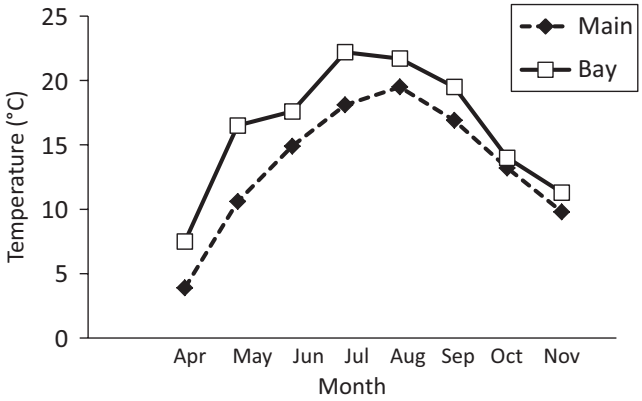

FIGURE 2 Water temperature inputs used for bioenergetics analysis of walleye in Saginaw Bay and the main basin of Lake Huron

3 | RESULTS

A total of 601 and 657 walleye stomachs were examined from Saginaw Bay and Lake Huron, respectively, of which 259 and 159 contained food. The mean ± *SD* length of walleye was 416 ± 63 mm

TABLE 1 Energy density of prey used for bioenergetics modelling for walleye in Saginaw Bay and the main basin of Lake Huron

Prey	Region	Energy density (J/g wet)	Source
Yellow perch	Saginaw Bay	4,720	Pothoven, Höök, and Roswell (2014)
Rainbow smelt		3,765	(Appendix) Saginaw Bay 2009–2011
Notropis spp.		5,172	(Appendix) Saginaw Bay 2009
Round goby		3,658	(Appendix) Saginaw Bay 2009–2010
Gizzard shad		4,301	(Appendix) Saginaw Bay 2009–2010
Other fish		4,512	Pothoven and Höök (2015) and Blouzdis et al. (2013)
Invertebrates		3,134	Cummins and Wuycheck (1971)
Yellow perch	Main basin	4,720	Pothoven et al. (2014)
Rainbow smelt		4,315	(Appendix) L. Huron 2007
Notropis spp		5,172	(Appendix) Saginaw Bay 2009–2011
Round goby		4,252	(Appendix) L. Huron 2007
Lake trout		5,256	Stewart, Weininger, Rottiers, and Edsall (1983)
Coregonid		5,802	(Appendix) L. Huron 2007–2009
Other fish		5,282	He et al. (2015)

in Saginaw Bay and 440 ± 74 mm in the main basin. Mean ± *SD* gut fullness was 0.013 ± 0.015 g food/g fish and did not differ between the bay and main basin in the early period ($F_{1,131}$ = 2.7, p = .10) or the late period ($F_{1,209}$ = 1.1, p = .29).

In the main basin of Lake Huron, diet assemblages did not differ among fish from the north and south regions (ANOSIM; p = .07, R value = .05), so they were combined for analysis to increase sample size, especially for the late period. In the early period, ANOSIM indicated that although diets were separated (p = .001), there was some overlap in diets between Saginaw Bay and the main basin (R value = .32). SIMPER indicated that differences between the two regions were due to round goby and rainbow smelt (Osmeridae, *Osmerus mordax*), which were more prevalent in diets in the main basin, and to invertebrates and yellow perch, which were more prevalent in diets in the bay (Table 2). In the late time period, ANOSIM indicated that although diets again differed among regions (p = .001), there was substantial overlap in diet assemblages (R value = .23). SIMPER indicated that the differences between regions were due mainly to round goby and rainbow smelt, which were more prevalent in diets in the main basin, and to gizzard shad (Clupeidae, *Dorosoma cepedianum*) and yellow perch, which were more prevalent in diets in the bay (Table 2).

In Saginaw Bay, the main prey by weight were yellow perch and rainbow smelt in the early period, but in the later time period, diet composition shifted towards gizzard shad as the main prey (Table 3). Although fish were the main prey, invertebrates did account for 9% of diet biomass in the early period, but <1% in the late period. In the early period, Chironomidae larvae and pupae accounted for 88% of the invertebrate biomass in diets, along with Amphipoda (6%), *Bythotrephes longimanus* (Cercopagididae, 3%) and Oligochaeta (2%). In the late period, invertebrates eaten were mainly Ephemeroptera nymphs (84%), along with Amphipoda (11%), *Bythotrephes longimanus* (3%), *Daphnia* spp. (Daphniidae, 2%) and Chironomidae (<1%). In the main basin of Lake Huron, the diet composition was dominated by round goby and to a lesser degree, rainbow smelt in the early period (Table 3). In the late period, diet composition was dominated by rainbow smelt and coregonids. There was a fairly high contribution of unidentified fish in the late period. Invertebrates accounted for <1% of the diet biomass in the early period and were not found in diets in the late time period. In the early period, the only two invertebrates eaten were Ephemeroptera nymphs (68%) and Cambaridae (32%). Only one alewife was found in walleye diets in the main basin, and none were found in walleye diets in Saginaw Bay.

In Saginaw Bay, almost half the walleye ate invertebrates in the early period, but only 5% in the late period (Table 3). In the early period, 80% of the fish that ate invertebrates consumed Chironomidae, whereas Ephemeroptera were eaten by 50% of the fish that consumed invertebrates in the late period. All other invertebrate groups were found in <25% of the fish that had consumed invertebrates in both time periods. In the early period, the most commonly eaten fish were yellow perch and rainbow smelt (>19%), and in the late period, gizzard

TABLE 2 Results from SIMPER analysis used to determine % contribution of prey species to dissimilarity in prey assemblages between walleye in Saginaw bay and the main basin of Lake Huron during an early (April–mid-June) and late (mid-June–November) time period in 2009–2011

Time period	Species	% Contribution
Early	Round goby	32
	Invertebrates	26
	Rainbow smelt	25
	Yellow perch	11
Late	Round goby	23
	Rainbow smelt	21
	Gizzard shad	21
	Yellow perch	15

TABLE 3 Diet composition (% wet weight) and frequency occurrence (%) of various prey for walleye in Saginaw Bay and the main basin of Lake Huron during an early (April–mid-June) and late (mid-June–November) time period during 2009–2011

		% Wet weight		Frequency %	
Period	Prey species	Bay	Main	Bay	Main
Early	Yellow perch	31	<1	19	1
	Rainbow smelt	29	28	24	41
	Notropis spp.	5	0	7	0
	Round goby	14	58	10	63
	Gizzard shad	0	0	0	0
	Lake trout	0	10	0	3
	Coregonid	0	2	0	1
	Alewife	0	0	0	0
	Other fish	0	1	0	1
	Unidentified fish	12	1	–	–
	Invertebrates	9	<1	48	2
	N examined			80	194
	N with food			46	92
	N with identifiable food			42	86
Late	Yellow perch	16	0	32	0
	Rainbow smelt	2	28	1	47
	Notropis spp.	3	1	11	6
	Round goby	8	6	18	44
	Gizzard shad	62	0	41	0
	Lake trout	0	0	0	0
	Coregonid	0	34	0	16
	Alewife	0	3	0	3
	Other fish	3	0	2	0
	Unidentified fish	6	28	–	–
	Invertebrates	<1	0	5	0
	N examined			521	463
	N with food			213	67
	N with identifiable food			158	32

shad, yellow perch and round goby were the most commonly eaten fish. In the main basin, the most commonly eaten prey were rainbow smelt and round goby in both periods (Table 3). Coregonids accounted for much of the diet biomass in the late period, but they were only eaten by 16% of fish.

The feeding strategy plots indicated that there was a high degree of specialisation by individuals in Saginaw Bay during both time periods (Fig. 3). Most points fell into the upper left quadrant, with no prey being overly dominant at a population level, that is individual walleye specialised on individual prey and each food category was consumed by a limited fraction (<50%) of predators. In the main basin, there was also a high degree of specialisation by individual walleye, but in the early period, round goby were specialised on by a majority of walleye, indicating they were a dominant prey at the population level in that period.

In Saginaw Bay, the largest prey eaten was gizzard shad, which was the only prey in diets from the bay with a mean length >100 mm, whereas the mean length of all other prey was <80 mm (Table 4). In the main basin, the mean length of lake trout (Salmonidae, *Salvelinus namaycush*) (157 mm) and coregonids (102 mm) found in stomachs both exceeded 100 mm, whereas that of rainbow smelt and round goby was <80 mm (Table 4). There was no difference in the total length of round goby (ANCOVA; $F_{1,121} = 0.7$, $p = .40$) or rainbow smelt (ANCOVA; $F_{1,44} = 0.2$, $p = .65$) consumed in Saginaw Bay and the main basin after adjusting for walleye length. These were the only two prey fish found in large enough quantities in both regions for comparison.

Assuming the same growth in all scenarios, consumption between April and November was 1,622, 1,338 and 1,460 g for an age-5 walleye in Saginaw Bay, in the main basin, and for a fish migrating from Saginaw Bay to the main basin respectively.

4 | DISCUSSION

We found that walleye in Saginaw Bay switched their diet in a different manner than walleye in the main basin of Lake Huron in response to the alewife collapse of 2003. Nonetheless, diet composition of walleye did undergo a major shift in both regions of Lake Huron in response to this dramatic change in the Lake Huron prey fish community, highlighting the flexibility of this apex piscivore. Alewives had previously been important in walleye diets in both Saginaw Bay (Fielder & Thomas, 2006; Haas & Schaeffer, 1992) and the main basin (N. Dobiesz, MS thesis, Michigan State University 2003), but were nearly absent from walleye stomachs in both regions during 2009–2011. However, walleye were able to quickly respond to this major ecosystem change by switching their diet to other species. Previous studies have also shown that walleye diets can shift rapidly in response to changes in the prey community (Haas & Schaeffer, 1992; Hartman & Margraf, 1992; Knight & Vondracek, 1993). Similarly, a resurgent population of striped bass (Moronidae, *Morone saxatilis*) along the Atlantic coast relied on different prey than prior to their recovery due in part to changes in the prey community (Walter & Austin, 2003).

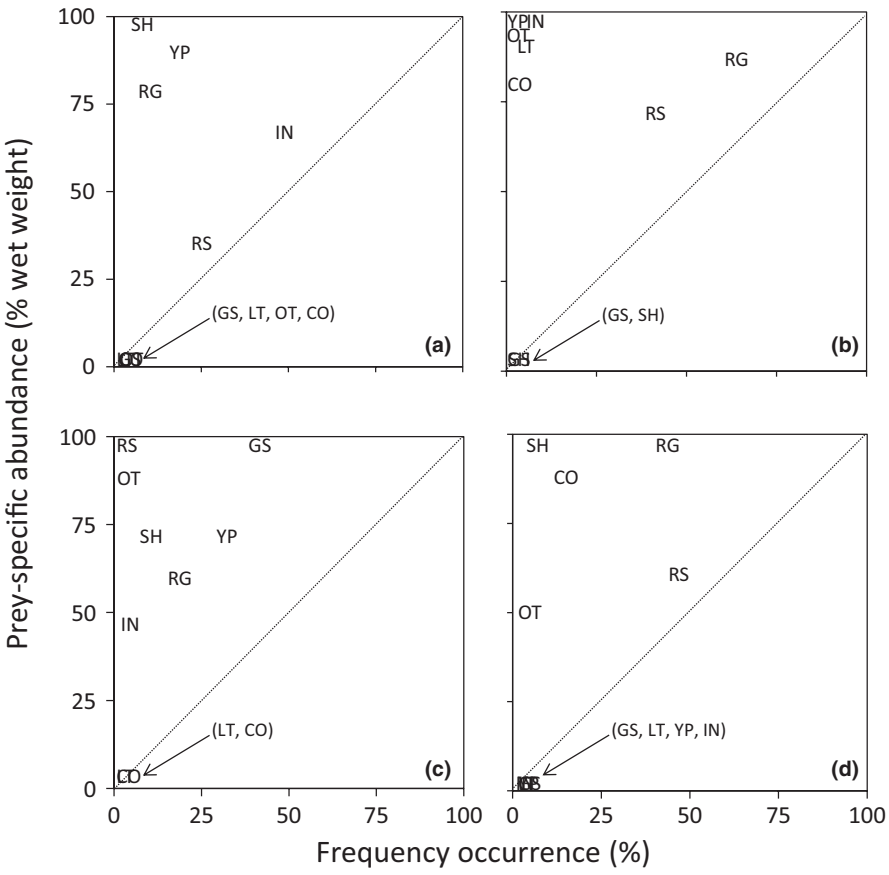

FIGURE 3 Feeding strategy plot (prey-specific abundance on a per cent wet weight basis plotted against frequency of occurrence, Amundsen et al., 1996) walleye; (a) =Saginaw Bay early period, (b) =main basin early period, (c) =Saginaw Bay late period, (d) =main basin late period. YP, yellow perch; GS, gizzard shad; RG, round goby; RS, rainbow smelt; SH, *Notropis* spp.; CO, coregonid; LT, lake trout; OT, other fish; IN, invertebrates. The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and unimportant prey in the lower left. The vertical axis represents the feeding strategy of the fish in terms of specialisation (upper part of plot) and generalisation (lower part of plot). Prey points in the upper left indicate specialisation by individuals, whereas points in the upper right indicate a dominant prey of the overall population (Amundsen et al., 1996)

TABLE 4 Total lengths of various prey found in walleye diets in Saginaw bay and the main basin of Lake Huron in 2009–2011

Region	Prey species	Mean ± *SD* (mm)	Range (mm)	*n*
Saginaw Bay	Gizzard shad	103 ± 22	56–146	58
	Rainbow smelt	79 ± 24	30–110	13
	Notropis spp.	70 ± 19	31–98	26
	Yellow perch	67 ± 25	27–166	100
	Round goby	59 ± 17	29–118	49
Lake Huron	Lake trout	157 ± 21	123–182	6
	Coregonid	102 ± 8	90–114	10
	Rainbow smelt	76 ± 17	52–141	37
	Round goby	70 ± 24	32–139	84

The predation pressures of a resurgent piscivore population can lead to new management issues by placing additional predation pressures on species that are also recreational or commercial targets (Hartman, 2003). In Saginaw Bay, age-0 yellow perch abundance increased following the collapse of the alewife populations (Fielder & Thomas, 2014; Ivan et al., 2011), providing an abundant source of prey for the resurgent walleye population. However, yellow perch are a spiny-rayed fish and are not considered a preferred prey of walleye (Hartman & Margraf, 1992; Knight & Vondracek, 1993). Historically, yellow perch were mainly important to walleye diets in Saginaw Bay when soft rayed fish such as alewife and gizzard shad were not available (Haas & Schaeffer, 1992). Prior to their collapse, alewife had provided a predation buffer throughout the year in Saginaw Bay (Haas & Schaeffer, 1992), whereas gizzard shad currently only provide a predation buffer in late summer and fall because they quickly grow beyond a consumable size after their first year of life (Knight & Vondracek, 1993). In turn, high predation by walleye on young yellow perch may now be a primary impediment towards yellow perch recruitment to older age classes and the recreational fishery in Saginaw Bay (Fielder & Thomas, 2014). Similarly, Hartman (2003) indicated that management might not be able to simultaneously manage for high populations of Atlantic coast striped bass and for high populations of their prey which also supported important fisheries.

Our study found that gizzard shad were more important to diets than Roseman, Schaeffer, Bright, and Fielder (2014), who used stomachs from angler caught fish in 2009–2011 to evaluate predator diets in Lake Huron. Although walleye from that study were caught throughout Lake Huron, most were from Saginaw Bay, and yellow perch, round goby and *Notropis* spp. (Cyprinidae) dominated diets (Roseman et al., 2014). One reason for the discrepancy is when fish were collected. In our study, all walleye that ate gizzard shad in Saginaw Bay were caught in September, and about 85% of the late period walleye from Saginaw Bay were caught in September. By contrast, most fish in the Roseman et al. (2014) study were caught prior to September. Thus, it appears that our study overestimated the importance of gizzard shad and the Roseman et al. (2014) study underestimated their importance.

There are limited historical data on walleye diets in the main basin of Lake Huron, but analyses from the 1990s indicated that alewife were the main component of the diet with only rainbow smelt making a substantial secondary contribution (N. Dobiesz, MS thesis, Michigan State University 2003). In our study, rainbow smelt were still an important diet component, but alewife have been replaced primarily by round goby (early period) or coregonids (late period). Although the abundance of rainbow smelt declined from 1994 to 2006, the decline was not to the same extent as the alewife decline (Riley et al., 2008). Round goby, a relatively recent source of food for piscivores, were initially found in Lake Huron in 1994 (Marsden, Jude, & Rudnicka, 1996) and increased in abundance between 1997 and 2003 (Schaeffer et al., 2005). Round goby have become an important diet component for other fish in Lake Huron, including lake trout (He et al., 2015; Roseman et al., 2014) and lake whitefish (Pothoven & Madenjian, 2013).

Piscivores can be an important regulator of the long-term dynamics of invasive prey species, and this interaction is critical for understanding invasion dynamics (Carlsson, Sarnelle, & Strayer, 2009). Predators that feed on an invasive prey types may have an advantage in disrupted ecosystems (Carlsson et al., 2009). Furthermore, in Lake Erie, eating non-native round goby has been linked to increased growth for some predators by providing a new pathway to access energy (i.e. invasive dreissenid mussels) that was not formerly available and because round goby, which consume invasive dreissenids, can be abundant and relatively easy to capture (Johnson, Bunnell, & Knight, 2005; Steinhart, Stein, & Marschall, 2004). In Lake Huron and Saginaw Bay, dreissenids account for about 30% of the diet biomass of round goby (S. Pothoven, NOAA and C. Foley, Purdue University, personal communication). This pathway of indirectly incorporating dreissenids into piscivore diets is becoming increasingly common throughout the Great Lakes (Dietrich, Morrison, & Hoyle, 2006; Johnson et al., 2005) and reflects a re-engineering of the littoral food web and a shift to more nearshore benthic pathways (Campbell et al., 2009; Hogan, Marschall, Folt, & Stein, 2007; Rush et al., 2012; Turschak & Bootsma, 2015; Turschak et al., 2014). Although round goby were eaten in both Saginaw Bay and the main basin, they were most prevalent in walleye diets in the main basin. In Lake Erie, walleye diets in 1994–2002 demonstrated less of a shift towards round goby consumption than other piscivores and walleye still mainly consumed pelagic prey (Johnson et al., 2005).

Two relatively high-energy prey types were eaten in the main basin: lake trout in the early period and coregonids in the late period. All coregonids that could be identified to species were bloater (Salmonidae, *Coregonus hoyi*), which recently saw a resurgence in recruitment in the lake (Roseman et al., 2015). Lake trout were the

largest prey found in walleye diets, but they were a relatively uncommon prey. However, Roseman et al. (2014) noted that predation by walleye and other predators could be an important source of mortality for stocked lake trout in Lake Huron. Coregonids were only eaten by 16% of walleye, but they accounted for >30% of diet weight in the late period. The recent resurgence in bloater recruitment in the lake (Roseman et al., 2015) could provide a high-energy prey in the main basin. Prior to their collapse in the mid-1900s, the coregonid cisco (Salmonidae, *Coregonus artedi*) provided a food source for walleye and a predation buffer for small yellow perch in Lake Huron, including Saginaw Bay (Ivan et al., 2011).

Walleye demonstrated a high degree of individual variation in diets, based on a large number of prey types falling in the upper left-hand corner of the feeding strategy plots (Fig. 3). Thus, almost no prey types were eaten by >50% of the fish, and the prey that were eaten generally accounted for the majority of the diet in those fish that ate that particular prey. Individual feeding variation is often overlooked in feeding studies, but is an important component to understanding population ecology (Svanbäck, Quevedo, Olsson, & Eklöv, 2015). Individual variation in diets can help reduce intraspecific competition and promote population stability during periods of high competition (Bolnick et al., 2003; Svanbäck & Persson, 2004). This could be particularly important for a population during a period of rapid recovery and exposure to a novel prey assemblage as occurred for walleye in Saginaw Bay.

Differences in water temperature regimes and diet composition between Saginaw Bay and Lake Huron's main basin have consequences for walleye feeding rates. Assuming similar growth rates, consumption by an age-5 walleye in Saginaw Bay was 18% and 10% higher than for an age-5 walleye in the main basin or for a migrating fish respectively. Walleye that spend some or all of the growing season outside of Saginaw Bay do not require the same amounts of food to achieve the same growth rates. Water temperatures in Saginaw Bay are warmer than in the main basin so metabolic rates are higher, requiring increased consumption to achieve similar growth rates. In addition, walleye diets in the main basin during the late period included a high proportion of the relatively high-energy prey, bloater. Differences in prey supply, walleye density (Hartman & Margraf, 1992) and water clarity (Lester, Dextrase, & Kushneriul, 2004) could affect walleye consumption rates, but were not accounted for in our simulation exercise. Furthermore, one assumes that there are costs associated with migrations that were not accounted for in the modelling exercise. However, the bioenergetics results do demonstrate the importance of different diet responses to consumption/growth for walleye following an ecosystem change.

The differences in walleye diets between Saginaw Bay and Lake Huron demonstrate this resurgent apex predator's ability to take advantage of varying prey assemblages in the face of environmental change. The flexibility of a predator like walleye can aid in its success (Bolnick et al., 2003; Schindler, Hodgson, & Kitchell, 1997), although there are limits (Nobriga & Feyrer, 2008). This flexibility also can produce new predator–prey interactions that can have implications for remaining prey, such as the potential impediment that predation now poses for a yellow perch recovery. Diet shifts can also lead to increased reliance on new energy pathways, such as the shift from a well-established, non-native pelagic prey (alewife) to a recently introduced benthic prey (round goby). These diet shifts ultimately affect our understanding of food web structure and energy pathways. Finally, the high degree of individual specialisation in diets, temporal variation and a high proportion of stomachs with no/unidentifiable prey provided challenges towards a better understanding of ongoing shifts in feeding habits and modelling the impacts of these changes for walleye. Future studies to determine the response of piscivores such as walleye to shifts in prey assemblages need to ensure that sampling can capture as much spatial and temporal resolution as possible in order to better evaluate the implications of ongoing changes in predator–prey dynamics.

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APPENDIX

Mean energy density (J/g wet) of prey species, region where fish were collected, and years that fish were collected. Energy density of fish was determined following protocols outlined in Pothoven et al. (2014). Briefly, individual fish were ground and dried for 3 days at 70°C and then further homogenised with a mortar and pestle. Entire homogenised fish (or a 1 g subsample for fish >1 g dry weight) were individually combusted in a Parr 1261 isoperibol calorimeter standardised with benzoic acid. For species where multiple years of samples were available for a given month, the mean was determined for that month across years and is reported. The average energy density across all months was used for bioenergetics simulations (see Table 1).

	Rainbow smelt Bay 2009–2011	Rainbow smelt Main 2007	*Notropis* spp. Bay 2009	Round goby Bay 2009–2010	Round goby Main 2007	Gizzard shad Bay 2009–2010	Bloater (coregonid) Main 2007–2009
April	4,238	–	–	–	–	–	–
May	4,133	4,295	4,028	3,392	4,478	–	6,690
June	–	–	–	–	–	–	–
July	–	3,964	5,700	3,692	3,911	–	5,905
August	–	–	5,302	–	–	3,970	–
September	–	–	5,001	3,890	–	3,825	–
October	3,004	4,687	5,831	–	4,368	5,108	4,812
November	3,685	–	–	–	–	–	–
Average	3,765	4,315	5,172	3,658	4,252	4,301	5,802
n	102	42	133	120	48	114	141